VII. *New Observations upon the Minute Anatomy of the Papillæ of the Frog's Tongue.* *By* LIONEL S. BEALE, *M.B., F.R.S., Fellow of the Royal College of Physicians, Professor of Physiology and of General and Morbid Anatomy in King's College, London; Physician to King's College Hospital, &c.*

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IN this paper I propose to give the results of some recent investigations upon the minute anatomy of the beautiful fungiform papillæ of the tongue of the little green tree-frog (*Hyla arborea*). The specimens have been prepared according to the principles laid down in former communications. The success I have met with in this and other minute anatomical inquiries is, I believe, almost entirely due to the process of investigation which I have adopted for some years past, and which enables me to render specimens very transparent, and to demonstrate all the tissues in one specimen. By this plan sections are obtained so exceedingly thin, without the destruction even of the most delicate tissues, that they may be examined under the highest powers which it is possible to obtain ($\frac{1}{26}$ magnifying 1700 linear, and $\frac{1}{50}$ magnifying about 3000 linear).

The following are among the most recent contributions to the anatomy of the papillæ of the frog's tongue:—

WALLER: "Minute structure of the Papillæ and Nerves of the Tongue of the Frog and Toad," Philosophical Transactions, 1847.

BILLROTH: "Ueber die Epithelzellen der frosch-zunge, sowie über den Bau der cylinder-und flimmerepithelien und ihr Verhältniss zum bindegewebe," Archiv für Anat. Physiologie, 1858, S. 163.

HOYER: "Mikroskopiche Untersuchungen über die zunge des Frosches," Archiv für Anat. Phys. 1859, S. 488.

AXEL KEY: "Ueber d. Endigungen d. Geschmäcksnerven in der zunge Frosches," MÜLLER'S Archiv, 1861, S. 329.

HARTMANN: "Ueber die Endigungsweise der nerven in den Papillæ-fungiformes der Froschzunge," Archiv für Anat. Phys. 1863, S. 634.

Although the views of AXEL KEY are supported by schematic figures which do not accurately represent the real arrangement of the tissues, they approach much nearer to the truth than those of other observers. He describes two kinds of cells at the summit of the papilla, epithelial and special cells concerned in taste. I have not been able to verify his statements in this particular. He has not demonstrated the peculiar network at the summit of the papilla which is seen so distinctly in my specimens, and his delineations of the prolongation of the axis-cylinder alone, and its divi-

sion into fibres far too fine to be visible by the magnifying powers employed, and the abrupt cessation of the white substance delineated by him, are evidently schematic,—indeed he does not pretend that the figures referred to are copies from nature. Still his inferences regarding the division of the nerve-fibres into very fine fibres which pass into the epithelium-like tissue at the summit of the papilla, approach much nearer to the actual arrangement than those of any other observers with which I am acquainted.

The latest researches upon the mode of termination of the nerves are by Dr. HARTMANN. These are concluded in the Number of REICHERT and DU BOIS-REYMOND'S 'Archiv' for 1863, which has only just been received in this country (June 1864). The drawings of the papillæ accompanying this memoir, especially fig. 65, plate 18, form an excellent illustration of how most beautiful and well-defined structures may be rendered quite invisible by being soaked in aqueous solution of bichromate of potash for three days, one day in carmine solution, and then in caustic soda!

In order that I may not express myself against the mode of preparation followed by this and many other observers in Germany in the present day more strongly than is justified by the results obtained as shown by their own drawings, I would refer to HARTMANN'S figure. Of this drawing it is not too much to say that it represents nothing sufficiently definite to enable any one to form an idea of the structure of the part. The drawing, and I conclude the preparation from which it was taken, are far behind the day; and it seems to me most remarkable that after all the anatomical research of the last twenty years an observer should publish such a figure as this as a representation of natural structure. The nerve-fibres are completely altered by the mode of investigation followed, and the finer fibres are of course destroyed or rendered invisible. Nor can I admit that the epithelium upon the summit of the papillæ represented in his fig. 64 gives a correct idea of this structure.

It may be proved conclusively by experiments that soaking delicate animal tissues in dilute aqueous solution of bichromate of potash renders invisible and destroys structures which can be demonstrated by other means. Inquiries conducted by the aid of such plans of preparation retard rather than advance anatomical inquiry, for some of the most important anatomical characters are rendered completely invisible. The very conflicting opinions now entertained by observers in Germany upon the structure of these papillæ, render it important that they should be studied again with the advantage of the highest powers, and the most advantageous methods of preparation which we now possess.

In this communication I shall only attempt to describe briefly those points which I believe to be new, and which are I conceive demonstrated in my specimens for the first time. Most of the points described in this paper were demonstrated more than eighteen months ago, and during this period the specimens have been repeatedly studied and shown to other observers. The points described can still be demonstrated in the same specimens (June 1864).

The structures entering into the formation of the papilla are the following:—

1. The connective tissue which forms the body of the papilla.
2. The "epithelium."
3. The nerve-fibres in the body of the papilla, and the fibres prolonged from them which form a plexus upon its summit.
4. Nerve-fibres ramifying in the connective tissue, upon the capillary vessels and amongst the muscular fibres.
5. The muscular fibres.
6. The vessels.

The Connective Tissue.

The nerves, vessels, and muscular fibres are imbedded in a very transparent basis-substance which exhibits a slightly striated or fibrous appearance when stretched, but this structure in all the papillæ of the Hyla is exceedingly delicate and transparent.

The great majority of the nuclei seen in this basis or connective substance are undoubtedly connected with the nerves, vessels, and muscular fibres, but there are a few which seem to belong to the connective substance alone, and may therefore be called "*connective-tissue corpuscles.*" It is possible that these at an earlier period may have been connected with nerves or muscles; they have descended from the same nuclei or masses of germinal matter as the nuclei taking part in the production of these tissues.

I consider that indefinite connective tissue of this kind results principally from the accumulation of the remains of higher structures, especially nerve-fibres, which were in a state of functional activity at an earlier period of life. At an early period of development nuclei (masses of germinal matter) can alone be detected. As development proceeds, tissue is formed by these nuclei, and increases as age advances. The large and fully-formed fungiform papillæ have twice as many nerve-fibres as smaller and younger ones. During the development of such an organ as one of these papillæ many changes occur, and much texture is produced and removed before the papilla attains its fully developed state. That passive substance called connective tissue which remains and occupies the intervals between the higher tissues, which possess active and special endowments, slowly accumulates, but undergoes condensation as the organ advances in age. Amongst this are a few nuclei which can no longer produce anything but indefinite "connective tissue" of the same character. In Plate XXI. fig. 9 it would have been impossible, had the specimen been prepared in the usual manner, to have determined if the nuclei marked *a*, *b* were nuclei of the muscle concerned in producing muscle, or connective-tissue corpuscles concerned in the formation of connective tissue only. This question requires restudy from a new point of view. It is quite certain that many of the nuclei figured in all my drawings in connexion with *nerves*, *vessels*, *muscles*, and *other tissues*, would, if the specimens had been prepared in a different manner, so

that their connexions were not so very distinctly seen, have been called "CONNECTIVE-TISSUE CORPUSCLES."

The drawings accompanying my paper explain the relation which I believe the essential structures entering into the formation of the papilla bear to the indefinite connective tissue in which they lie imbedded.

Epithelium.

The so-called epithelium upon the summit of the papilla of the frog's tongue (Plate XXI. fig. 1, *a*) differs from the epithelium attached to its sides (*b*), that covering the simple papillæ (*c*), and that on the surface of the tongue generally, in many important characters. As is well known it is *not ciliated*. The cells differ from the ciliated cells in several points. They are smaller than these. The nucleus is very large in proportion to the entire cell. The cells are not easily separated from one another, as is the case with the ciliated epithelium. These cells form a compact mass, the upper surface of which is convex. This is adherent by its lower surface to the summit of the papilla, and it is not detached without employing force. The cells do not separate one by one, as occurs with the ordinary epithelium, but the whole collection is usually detached entire, and it is I believe *torn away*.

Although some observers would assert that the two or three layers of cells represented in my drawings do not exist, but that the appearance is produced by the cells of a single layer being pushed over one another by pressure, I am convinced that in this mass upon the summit of the papilla of the Hyla there is more than the single layer of cells represented by HARTMANN, who is the latest observer on this point.

HARTMANN'S representation (*l. c.*) of this very same structure from the summit of the papilla of the Hyla is very different from my drawings. Not only do we represent these same cells of very different shapes, but the nucleus in my specimens is three or four times as large in proportion to the cell as represented by him.

The general outline of the free surface is convex (*a*, *a*, *a*, fig. 1, Plate XXI.), and the tissue which intervenes between the nuclei appears very transparent and projects a little, so as to give the convex summit a honeycombed appearance (Plate XXI. fig. 7).

The under concave surface of this hemispheroidal mass which adheres to the summit of the papilla of the Hyla's tongue, corresponds to the exact area over which the nerve-fibres of the papilla are distributed, as will presently be shown. The shape of these cell-like bodies, of which the mass is composed, and their connexion with fibres is shown in Plate XXI. fig. 3, and in the very highly magnified specimen represented in fig. 2. After the examination of a vast number of specimens I think these figures represent the actual arrangement, but this point is most difficult of investigation. In the intervals between what would be called, if they were capable of complete separation from one another, the individual cells, fibres are seen. These fibres do not I think arise simply from the pressure to which the masses have been subjected. I have represented the

arrangement as I believe it to be in Plate XXI. fig. 6, from the central part of one of the hemispheroidal masses. I regard the entire hemispheroidal mass as resembling in its essential structure the network I have described at the summit of the papilla, but the masses of germinal matter are so very close together and the fibres so much interlaced with one another, that it is most difficult to unravel the mass without destroying it. The arrangement at the surface is seen in Plate XXI. fig. 7.

The epithelium of the tongue generally is easily removed, but many of these hemispheroidal masses remain connected with the summits of the papillæ to which they belong. From what I have stated, it will I think be admitted that the constituent parts of the mass at the summit of the papilla could not be properly called epithelial cells, so that, with reference to the termination of the nerves in the papilla, I think it is more correct to say that nerves may be traced to special bodies or cells which form a hemispheroidal mass attached to the summit of the papilla, than to assert that the separate bodies, which compose the mass in which nerves terminate, are actual epithelial cells.

In the simple papillæ (Plate XXI. fig. 1, *d*) of the frog's tongue, a "nucleus" of a nerve sometimes projects beyond the outline of the papilla and lies amongst the epithelium. This nucleus, however, adheres to the papilla when all the epithelial cells have been detached. It might from its position be easily mistaken for an epithelial cell, but it is no more really related to this structure than is a ganglion-cell, or a caudate nerve-cell of the spinal cord. The cells of the ciliated epithelium of the frog's tongue are not in any instance, as far as I am able to observe, connected with the nerve-fibres. It is probable that the opposite inference, which is still held by many observers, has resulted from the observation of such a nucleus as is represented in Plate XXI. fig. 1, *d* projecting beyond and adherent to the surface of the papilla. It is really continuous with the delicate nerve-fibres (*e*) ramifying in the substance of the papilla, but it is not an epithelial cell, and remains adherent after every particle of epithelium has been removed.

The nervous tissue is in all cases structurally distinct from every other tissue, in every part of its distribution. It never blends with epithelium any more than it blends with fibrous tissue, cartilage, bone, or muscle. If nerves exert any direct influenee upon the nutrition of any of these tissues, the influence must be exerted through some distance. The results of anatomical research render any physiological doctrine which maintains that nerves act through their structural continuity with other tissues untenable. My own observations lead me to conclude that nerves do not directly influence the processes of nutrition, growth, or development at all. They act only indirectly, and affect the supply of nutrient matter distributed by modifying the calibre of the vessels, and hence regulate the supply of blood which passes to the capillaries. The nerves I believe really exert their influence upon the contractile muscular coat of the small arteries and veins alone, and do not act directly upon any other tissues.

The Nerves.

With regard to the trunks of the nerves, I remark the following facts of importance:—

1. That the bundle of nerve-fibres distributed to a papilla always divides into two bundles which pursue opposite directions. The division of the bundle may take place just at the base of the papilla, or at some distance from it, but it always occurs (Plate XXI. fig. 1).

2. Fine pale nerve-fibres pass from the same trunk of dark-bordered fibres as that which gives off the bundle of nerves to the papilla. The fine fibres ramify—

a. Amongst the muscular fibres of the tongue (Plate XXI. figs. 1, 9).

b. Upon the vessels (Plate XXI. fig. 1, *i*, *i*, *i*).

c. In the connective tissue of the tongue generally, and also in the simple papillæ (Plate XXI. fig. 1, *d*, *e*).

The division of the bundle at the base of a papilla is shown in Plate XXI. fig. 1, and in Plate XXII. fig. 10 is a diagram to indicate the manner in which the nerve-plexuses at the summits of the papillæ are connected together by commissural fibres. Thus in action the papillæ may be associated together. The bearing of this arrangement upon the existence of complete nervous circuits is discussed in my 'Archives,' vol. iv. The bundle in the central part of the papilla consists of dark-bordered fibres, which frequently cross and interlace with one another in this part of their course. They vary much in diameter, some being so fine as scarcely to be visible.

As the bundle passes towards the summit of the papilla, the individual fibres divide and subdivide into finer branches. Now, as I have before remarked, nerves so near their distribution as these do not usually possess an axis-cylinder as a structure distinct from the white substance. The white substance does not abruptly cease, while the axis-cylinder is alone prolonged onwards by itself as is often described, but the entire fibre divides and subdivides. In fact dark-bordered nerve-fibres, near their ultimate ramifications, always consist of fatty albuminous material imbedded in a transparent matrix of connective tissue. The "tubular membrane," "white substance," and "axis-cylinder" can never be demonstrated as distinct structures near the peripheral distribution of nerves. The "tubular membrane" is nothing more than the transparent matrix in which one or more nerve-fibres are imbedded.

The dark-bordered fibres divide into finer fibres about the level of the ring or half-ring of capillaries at the summit of the papilla. As the fibres are exceedingly transparent, they are usually lost from view about this point. For example, HARTMANN'S figures convey the idea that distinct dark-bordered fibres can be followed as high as this point, but that they cannot be traced further. Above this spot the papilla is a little thickened and the tissue more granular, and hence it is not to be wondered at that great difficulty should have been experienced in demonstrating the further course of the nerves, or that many different views should be entertained upon the oft debated question of the mode

of ending of nerves in this situation; but it is most certain that the fibres do divide and subdivide into finer and much more transparent fibres at this point, and that these again divide and subdivide and form an elaborate plexus in the summit of the papilla, which has not been before described.

By reference to the figure, the arrangement, which is not easily described with accuracy, will be at once understood, so that a minute description of it would be superfluous.

Above the plexus *c* (Plate XXI. fig. 3), and below the epithelium-like organ at the summit of the papilla (*a*), is a layer (*b*) which appears to be composed of granular matter. In my most perfect specimens, however, this "granular layer," when examined by very high powers under the influence of a good light, is seen to consist of a plexus of extremely fine fibres which interlace with one another in every direction, but which pass from the plexus above to the epithelium-like nervous (?) organ upon the summit of the papilla (Plate XXI. fig. 2). I believe this granular appearance to result from the extreme delicacy and fineness of the nerve-fibres at this part of their course. In like manner the "granular matter" seen in the grey matter of the cerebral convolutions and that of the retina, results mainly from the breaking down of very fine and delicate nerve-fibres, which undergo disintegration very soon after death, unless they are subjected to special methods of preparation.

Of the existence of the elaborate network of nerve-fibres with the large nuclei, represented in Plate XXI. fig. 3 *c*, there can be no question whatever; but there may be some difference of opinion regarding the exact relation of the very fine nerve-fibres at the summit of the papilla, to the peculiar cells which surmount it, and the nature of the granular matter just described. However, there are but two possible arrangements:—

1. That the nerves form a network of exceedingly fine fibres upon the summit of the papilla, upon which the bases of the epithelium-like cells impinge.

2. That the very fine nerve-fibres are really continuous with the peculiar and epithelium-like cells; in which case these bodies must be regarded as part of the nervous apparatus.

There seems to me to be so much strong evidence in favour of the last view, that I venture to express a decided opinion that this is the truth. In many specimens I have seen, and most distinctly, the delicate network of fibres represented in Plate XXI. fig. 3 continuous with the fine nerve-fibres in the summit of the papilla, and I have demonstrated the continuity of these fine fibres with the matter of which the outer part of these peculiar cells consists (Plate XXI. figs. 2, 3, 6). I have also seen what I consider to be nerve-fibres in the intervals between some of these cells (Plate XXI. fig. 7). Upon the whole I am justified in the inference that there is a structural continuity between the matter which intervenes between the masses of germinal matter at the summit of the papilla and the nerve-fibres in its axis, and I consider that an impression produced upon the surface of these peculiar cells may be conducted by *con-*

tinuity of tissue to the bundle of nerve-fibres in the body of the papilla. These peculiar cells in the summit of the papilla cannot therefore be regarded as epithelium, and the mass constitutes a peculiar organ which belongs not to epithelial structures, but to the nervous system.

Although there can be no doubt whatever as to the existence of an intricate and exceedingly delicate nervous network or plexus at the summit of every papilla, such a plexus might be connected with the nerves according to one of two very different arrangements:—

1. The plexus might be formed at the extremity of a nerve or nerves, as represented in diagram (Plate XXII. fig. 17).

2. The plexus might form a part of the course of a nerve or nerves, as represented in diagram (Plate XXII. fig. 18).

If the first be true, the network must be terminal, and impressions must be conveyed along the fibre, of which the plexus is but the terminal expansion, direct from periphery to centre. If the second arrangement is correct, the network forms a part of a continuous circuit or of continuous circuits. I believe the division of the nerves at the base of the papilla, already adverted to, is alone sufficient to justify us in accepting the second conclusion as the more probable; but when this fact is considered with reference to those which I have adduced in my paper published in the 'Transactions' for 1863, and that in the 'Proceedings' for June 1864, and the observations published in several papers in vols. ii., iii., and iv. of my 'Archives,' and in the Croonian Lecture for 1865, I think the general view in favour of complete circuits is the only one which the anatomical facts render tenable. The mode of branching and division of trunks and individual fibres is represented in Plate XXII. figs. 20, 21, 22, 23.

From the number and size of the nerve-fibres constituting the bundle in the centre of the papilla, we should infer that the finest ramifications resulting from the subdivision of these branches would be very numerous, since it has been shown that the fine fibres resulting from the subdivision of a *single* dark-bordered fibre in the frog's bladder, palate, skin, and muscle, constitute plexuses or networks which pass over a very extended area. The mode of formation of a nerve-plexus is represented in Plate XXII. figs. 11 & 14. In these beautiful little organs the numerous fibres resulting from the subdivision of the dark-bordered fibres are distributed over a comparatively small extent of tissue, forming the summit of the papilla. Still we have the same formation of plexuses, the constant change in the direction taken by fibres, and the same crossing and intercrossing which have been noticed in other situations. In fact the nervous distribution in these organs presents the same typical arrangement as is met with in other tissues, but it is compressed into a very small space.

Now with regard to the epithelium-like structure upon the summit, it has been shown that the nerve-fibres are probably continuous with the material lying between the large nuclei. In fact if the interpretation of the appearances which I have given be correct, the arrangement may be expressed thus:—

The material marked *a* (Plate XXI. fig. 2) is a continuation of the nervous structure or tissue, while the matter marked *b* bears the same relation to this as the so-called nucleus of a nerve bears to its fibre, of an epithelial cell to its wall. If this be so, the matter which is freely exposed at the very summit of the papilla is at least structurally continuous with nerve-tissue, if it is not to be regarded as nerve itself. My own opinion is that it is just as much nerve-tissue as a fine nerve-fibre is nerve-tissue, or the caudate process of a nerve-cell is nerve-tissue. The formed matter is produced by the large masses of germinal matter which are so very numerous, just as the formed matter of a central nerve-cell results from changes occurring in its germinal matter.

It may not be out of place here to consider how the elaborate organ connected with the bundle of nerve-fibres of the papilla may act during life. As already stated, the free surface is uneven, and the arrangement is such that there are many elevations projecting, like fibres, by slightly varying distances, from the general surface. Now from the intricate interlacement of the nerve-fibres in the summit of a papilla, as well as at the point between this and the peculiar organ (Plate XXI. fig. 3, *b*), it is obvious that a fibre given off from one coming from the extreme left of the papilla, for example, may be situated a very short distance from a fibre coming from the opposite side. Any object, therefore, which connects the exposed projections would produce a temporary disturbance in the nerve-currents which are traversing these fibres, and this alteration in the current would of course produce a change in the cell or cells which form part of the same circuit in the nerve-centre. Any strong pressure would influence all the fibres distributed to this delicate nervous organ.

The supposed mode of action is explained by the plan (Plate XXI. fig. 4).

Nerve-fibres ramifying upon the capillary vessels, in the connective tissue, and upon the muscular fibres.

Many of the so-called connective-tissue corpuscles, with their anastomosing processes or "*tubes*," are really nerve-nuclei and very fine pale nerve-fibres, as has already been shown in observations upon the frog's bladder. In the tongue I have followed these fine fibres in very many specimens. They can only be seen and traced in specimens prepared in syrup, glycerine, or other viscid medium miscible in all proportions with water.

In Plate XXI. fig. 1, *f*, and in fig. 8, one of these fine branches, coming off from a bundle of dark-bordered fibres, is represented. Now, if examined by a low power, this might be mistaken for a fibre of connective tissue; but it really consists of several very fine fibres, which in their arrangement exhibit the same peculiarities observed in nerves ramifying in larger trunks (Plate XXII. figs. 20, 23). The fine branches divide and subdivide, and the delicate fibres resulting from their division can be followed for a very long distance. The finest are composed of several finer fibres, and they form networks or plexuses, the meshes of which vary much in size.

The branches which are distributed around the capillaries, in the connective tissue,

and to the musular fibres, seem to result from the division and subdivision of the same fibres (Plate XXI. fig. 1).

Nerves which are constantly distributed external to the capillary vessels and in the connective tissue have been demonstrated by me (Plate XXII. fig. 15) (see Archives, vol. iv. page 19). I consider these fibres as the afferent fibres through which an impression conveyed from the surface or from the tissues around capillaries, influences the motor nerves distributed to the small arteries from which the capillaries are derived. It is probable that these nerve-fibres pass to the very same set of central cells as that from which the vaso-motor fibres take their rise. It is through these fibres that changes in the nutrition of the tissues may affect the circulation in the neighbouring vessels.

In these fungiform papillæ, then, there are

1. The bundle of nerve-fibres which is distributed to the sensitive nervous organ at the summit.

2. Delicate fibres which may be traced to fibres running in the same bundles as purely sensitive fibres. These delicate fibres are distributed

a. Around the capillaries of the papilla (Plate XXI. fig. 1, *i*). See also Plate XXII. fig. 15.

b. Some fibres ramify in the connective tissue of the simple papillæ (Plate XXI. fig. 1).

c. Some are distributed to the muscular fibres (Plate XXI. figs. 1 & 9).

Now the first and second fibres are probably sensitive, excitor, or afferent, whilst the last must be motor. From this observation it follows that certain afferent and motor fibres are intimately related at their distribution, a conclusion already arrived at in my investigations upon the distribution of the nerves to the frog's bladder, the palate, and pharynx. Moreover I think that fine fibres passing from the plexus of sensitive fibres at the summit of the papilla, establish here and there a structural continuity between these and the fibres ramifying in the connective tissue and around the capillary vessels. It is very difficult to obtain a specimen which renders this perfectly certain, but I have been led to a similar conclusion in investigations upon the corpuscula tactûs of the human subject. The physiological interest and importance of this branch of anatomical inquiry are so great, and it promises to lead to such important results, that it cannot be too minutely or too patiently worked out.

Of the Muscles.

The muscular fibres of the papilla (Plate XXI. fig. 1) are the continuations of muscular fibres in the substance of the tongue. They are excellent examples of branching striped muscle. The finest branches are less than $\frac{1}{50,000}$th of an inch in diameter, but these exhibit the most distinct transverse markings. The markings, however, gradually cease, and the fibre becomes a mere line, which is lost in the connective tissue at the summit of the papilla. The arrangement will be understood if Plate XXI. figs. 1 & 9 be referred to.

The so-called nuclei or masses of germinal matter in connexion with these fine muscular fibres present several points which will well repay attentive study. These masses of germinal matter are sometimes twice or three times the width of the fibre with which they are connected. In a paper published in Part XIV. of my 'Archives,' I have adduced facts which render it probable that these nuclei or masses of germinal matter change their position in a very remarkable manner during life.

The conclusions I have arrived at upon this point are as follows:—

The masses of germinal matter appear to move along the surface of the already-formed muscular tissue, and as they move part of their substance becomes converted into muscle (Plate XXII. fig. 13). It is in this way that new muscle is formed and new muscular tissue is added to that already produced. The germinal matter itself does not diminish in size, because it absorbs as much pabulum as will compensate for what it loses of its own substance by conversion into tissue. In the young muscle the nucleus increases in size.

From what I have observed, I think that these oval masses of germinal matter move in different directions, but always in a line with the fibrillated structure, so that in a muscle some will be moving upwards, some downwards; and when the nuclei are arranged in rows or straight lines, the nuclei lying in adjacent lines will be moving in opposite directions. During the formation of a muscle these masses undergo division in two directions, longitudinally and transversely. The two masses which result from the division of one will pass in opposite directions.

As is well known, the position of these nuclei with respect to the formed muscular tissue is very different in different cases. Sometimes they are in the very centre of the elementary fibre, as in the constantly-growing fibres of the heart, sometimes upon its surface only, sometimes distributed at very equal distances throughout its substance. Wherever these nuclei are situated new muscular tissue may be produced, and it is only in these situations that muscular tissue ever is produced; so that by the position of the nuclei we learn the seat of formation of new muscle at different periods of life.

The facts which I regard as favourable to the view above expressed concerning the movements of the masses of germinal matter of muscle, are derived from many sources, but I will refer to some observed in the case of the muscles of the papillæ of the tongue. Here the muscular fibre is very thin and delicate, and very favourable for observation. The mass of germinal matter is very much wider than the muscle. Often three or four of these masses are seen close together (Plate XXI. fig. 9), while for some distance above and below the muscular fibre is destitute of nuclei. The narrowest extremity of the oval mass is directed in some cases towards the terminal extremity of the muscle, in others towards its base. There are often three or four fine fibres branching off from one stem, and gradually tapering into fine threads towards their insertion at the summit of the papilla (Plate XXI. figs. 1 & 9). The nuclei are three or four times as wide as these fibres. The greatest difference is observed in the distance between contiguous nuclei

connected with the very same fibre. If the muscle had gone on growing uniformly in all parts since the earliest period of its development, the nuclei would be separated from one another by equal distances, or by distances gradually but regularly increasing or diminishing from one extremity of the fibre towards the other.

I think the irregular arrangement of the nuclei in these muscular fibres of the tongue is to be accounted for by their movements. Perhaps, of a collection of these nuclei close together, two may be moving upwards towards the narrow extremity of the muscle which is inserted into the connective tissue, while the third may be moving in the opposite direction.

In some instances a "fault" is observed in the production of the muscular tissue, as if the nucleus had bridged over a space and formed a thin layer or band of muscular tissue, which, when fully formed, was separated by a narrow space or interval from the rest of the muscle. See Plate XXII. fig. 12.

In cases in which the nuclei are distributed at intervals throughout the muscular tissue, as in the large elementary fibres of the muscles of the frog, the formation of the contractile material gradually ceases as the elementary fibre attains its full size. When this point has been reached some of the nuclei gradually diminish in size, and their original seat is marked by a collection of granules. These granules are sometimes absorbed, and the seat of the original nucleus is marked by a short line which gradually tapers at the two extremities until it is lost.

It is almost needless to say that no alteration produced by the different contractions of the muscle in different parts, would account for the position of the nuclei observed in the fine fibres of the papillæ of the frog's tongue.

These views, it need scarcely be said, differ entirely from those generally entertained upon the development and formation of muscular tissue. They are supported by detailed observations made in all classes of animals, and in the same species at different periods of age. There are some facts in connexion with the changes occurring in disease which afford support to this view, which involves three positions. That in the nutrition of muscle the pabulum invariably becomes converted into germinal matter; that the latter undergoes change, and gradually becomes contractile tissue; and that all the contractile material of muscle was once in the state of the material of which the nuclei or masses of germinal matter are composed. It is not deposited from the blood, nor produced by the action of the nuclei at a distance, but it results from a change in the very matter of the nucleus itself. The manner in which this occurs has been already discussed in the paper above referred to (Archives, No. XIV.). It was shown that the oval nucleus could be followed into a very fine band of contractile tissue or fibrilla (Plate XXII. fig. 13). We pass from the matter of the nucleus into very transparent imperfectly-formed tissue in which no transverse lines are perceptible, and from this into fully-developed contractile material in which the characteristic transverse markings are fully developed.

Of the Capillaries.

The capillaries of the papilla of the frog's tongue are remarkable for their large size. In the common frog there is a complete vascular ring at the summit of the papilla, through which the bundle of nerve-fibres distributed to this part pass. In the Hyla the same is observed in some of the papillæ, but the more common arrangement may be described as a half ring or a simple loop, bent upon one side at its upper part (Plate XXI. fig. 1).

When the large capillaries of the papilla are distended with transparent Prussian-blue injection, their walls are seen to be of extreme tenuity and transparency. Connected with the transparent tissue are numerous oval masses of germinal matter (nuclei), which are separated from one another by very short intervals. Some of these masses project slightly from the inner surface of the vessel into its interior, but the majority seem to be upon its external surface. Of an oval form, many of these latter gradually taper into thin fibres which are continuous with the tissue of which the vascular wall is constituted. The delicate membrane constituting the vascular wall exhibits longitudinal striæ, which are probably produced in its formation, and by its external surface is connected with the delicate connective tissue which forms, as it were, the basis-substance of the papilla, and intervenes between all the important tissues which are found in it. This is proved by the fact that the vessel is moved when the transparent connective tissue at some distance from it is drawn in a direction from the vessel.

The most interesting point I have observed in connexion with the anatomy of these vessels, is the existence of very fine nerve-fibres. These form a lax network around the capillary. I have traced these fine fibres continuous with undoubted nerve-trunks in many instances, and have followed the latter into the trunks of dark-bordered fibres, from which the bundle in the papilla is derived. A similar arrangement of fine nerve-fibres has been demonstrated in connexion with other capillary vessels of the frog. These fine nerve-fibres are very distinct in several of my specimens.

I have indeed observed, in my paper published in the Transactions for 1863, contrary to the statements of most anatomists, that capillary vessels generally are freely supplied with nerves, but the latter and their nuclei have been regarded as connective-tissue fibres and connective-tissue corpuscles; I have shown in certain specimens that, of the two fibres resulting from the subdivision of a dark-bordered fibre, one was distributed to the fibres of voluntary muscle, while the other ramified over the vessels supplying the muscle (Plate XXII. fig. 15). These facts, it need scarcely be said, are of great importance with reference to the mechanism of nervous action.

I have not succeeded in demonstrating lymphatic vessels in the papillæ of the frog's tongue.

Besides the various nuclei described, there are several round, oval, and variously-shaped bodies, about the size of a frog's blood-corpuscle, which are composed principally of minute oil-globules and granules. These are not coloured by carmine. Many

contain a small mass of germinal matter (nucleus) in the centre, which is of course coloured. In some of the smaller ones this mass of germinal matter is much larger in proportion to the entire "cell." These bodies resemble many of the fat-cells of the frog, and I think it probable they are of this nature. It is, however, possible that these masses may be altered lymph-corpuscles. The Hylæ which I examined had been for some time in confinement, and contained very little adipose tissue.

Conclusions.

1. That fine nerve-fibres ramify in the connective tissue of which the simple papillæ are composed, and that connected with these nerve-fibres are oval masses of germinal matter or nuclei, which are usually regarded as "connective-tissue corpuscles."

2. That neither the epithelial cells of the frog's tongue generally, nor those covering the simple papillæ, are connected with nerve-fibres.

3. That the mass consisting of epithelium-like cells upon the summit of the fungiform papilla, is connected with the nerve-fibres, but it is not an epithelial structure.

4. That the dark-bordered sensitive fibres constituting the bundle of nerves in the axis of the papilla divide near its summit into numerous very fine branches, with which nuclei are connected. Thus is formed a plexus or network of exceedingly fine fibres upon the summit of each papilla; from this network numerous fine fibres may be traced into the special *nervous* organ, composed of epithelium-like cells upon the summit, with every one of which nerve-fibres appear to be connected.

5. That the bundle of nerve-fibres distributed to a papilla always divides into two bundles which pursue opposite directions. The division of the bundle may take place just at the base of the papilla, or at some distance from it, but it always occurs.

6. That fine pale nerve-fibres pass from the same trunk of dark-bordered fibres as that which gives off the bundle of nerves to the papilla. The fine fibres ramify—

a. Amongst the muscular fibres of the tongue.

b. Upon the vessels.

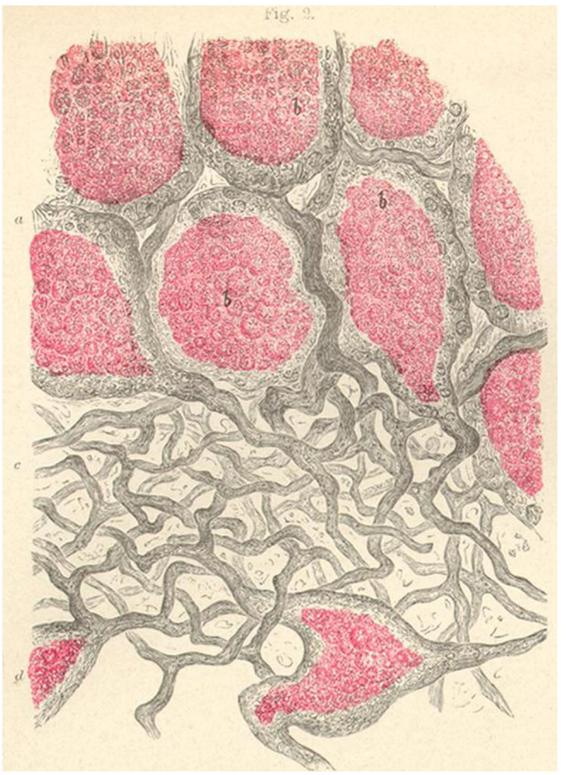
c. In the connective tissue of the tongue generally, and also in the simple papillæ.

7. That the fine nucleated nerve-fibres ramify freely amongst the delicate branching muscular fibres of the papillæ, and form plexuses or networks which exhibit no nerve-ends or terminations, nor in any case does a nerve-fibre penetrate through the sarcolemma or investing tissue of the fibre, or connect itself with the nuclei of the muscle. As many of the muscular fibres are so very fine and narrow, the distribution of the nerves, and their exact relation to the contractile tissue, can be demonstrated very distinctly in the case of the muscles of the papillæ of the frog's tongue.

Description of the Plates.

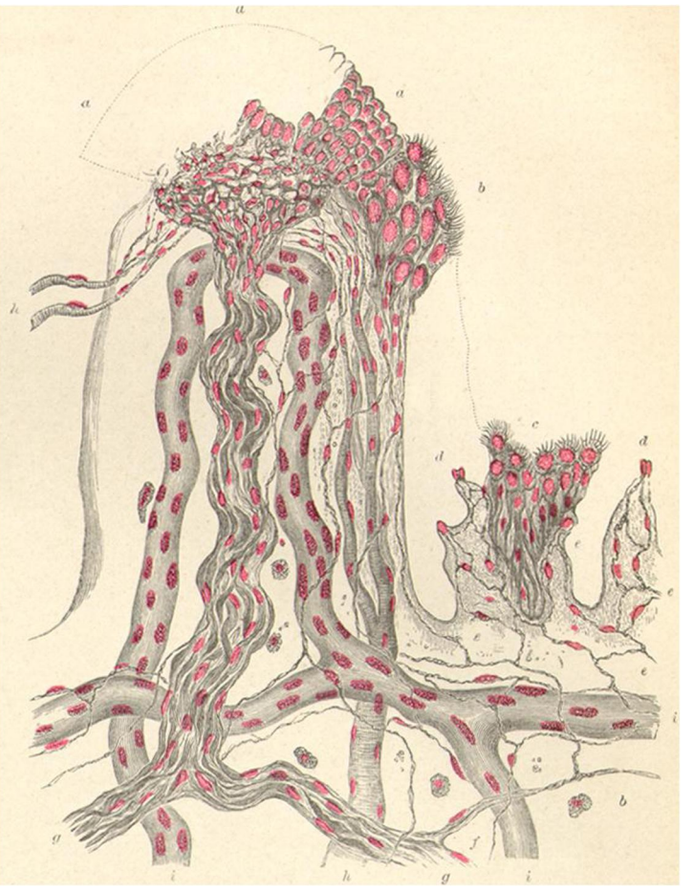
The figures represented in Plate XXI. illustrate the structure of the papillæ of the frog's tongue. In fig. 1 an entire fungiform papilla only in part finished is delineated. A portion of every tissue entering into its formation is however represented. The structure of this papilla is most interesting, because in a very small space we have *epithelium, muscle, connective tissue, nerves of special sensation, motor nerves, distributed to the branching muscular fibres, and nerves distributed to the capillary vessels and connective tissue which are probably afferent.* In the other figures the most important structures entering into the formation of the papilla are represented very highly magnified. Many of the preparations from which these drawings have been taken are in my possession, and can be examined by any one desirous of seeing them. The mode of preparation adopted is special, and has been referred to very generally in previous papers. It is described in detail in 'How to Work with the Microscope.' Each figure is fully explained in the text beneath it, so that it is unnecessary to give a more minute description of the illustrations in this or the following Plate.

Fig. 2.



Small portion of the plexus of nerve fibres at the summit of the papilla, showing the connection of the nerve fibres with the cells. × 500. *a*. Epithelium-like cells upon the summit, as in Figs. 1, 3 and 4. *d*. Triangular cells connected with delicate nerve fibres. *b*. Germinal matter of epithelium like cells on summit. The plexus *c* corresponds to that marked *b* in Fig. 3.

Fig. 1.

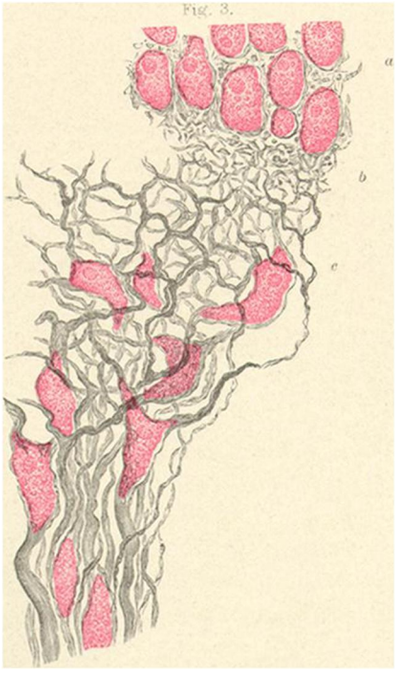


Fungiform and simple papillæ of tongue of the Hyla. *a*. Epithelium-like mass at summit of papilla. *b*. Ciliated epithelium at the sides of the papilla. *c*. Ciliated epithelium, covering simple papillæ. *d d*. Summits of two simple papillæ, with nuclei connected with the nerves projecting from them. *e*. Fine nerve fibres with their nuclei in the connective tissue. *f*. Fine nerve fibres which may be traced to the nerve trunk *g*. *h*. Muscular fibres freely branching, the tendinous prolongations of the finest sub-divisions being inserted into the connective tissue at the summit of the papilla. *i*. Capillary with its nerve fibres. × 215

Fig. 4.

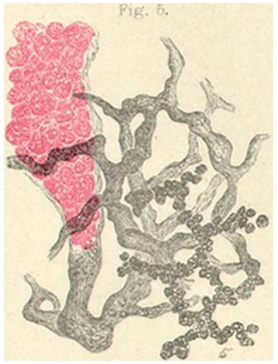
Diagram to shew the supposed arrangement of the nerves and their connection with the cells on the summit of the papilla.

Fig. 3.



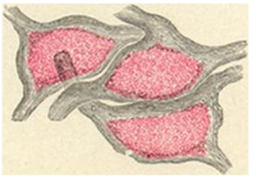
Portion of the central stem of nerve fibres, breaking up to form the nerve plexus at the top of the papilla. *a*. Epithelium-like cells upon the summit of the papilla. *b*. Intricate interlacement of finest nerve fibres immediately below, highly magnified at *c* Fig. 2. *c*. Expansion of nerve fibres in the form of a net-work on the top of the papilla. × 1700.

Fig. 5.



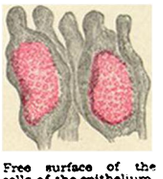
A portion of one of the triangular cells or nuclei connected with the fine nerve fibres, forming the plexus, at the top of the papilla, as seen after the removal of the epithelium-like mass from the summit. The fine fibres upon the surface are those which pass to the epithelium-like mass on the summit. × 600.

Fig. 6.



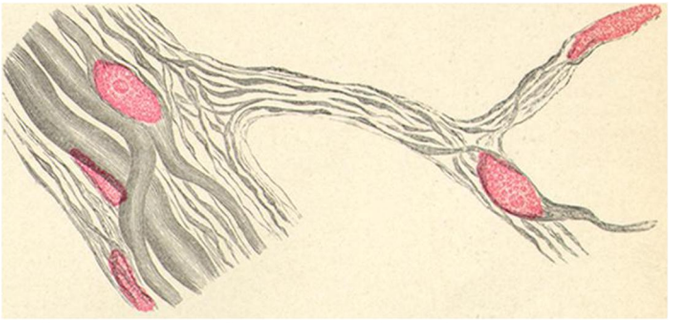
Three cells from the epithelium-like mass upon the summit of the papilla. × 300.

Fig. 7.



Free surface of the cells of the epithelium-like mass at the summit of the papilla. × 300.

Fig. 8.



Fine nerve fibres coming off from a trunk, to be distributed to muscles, vessels and connective tissue, near the base of a papilla as at *f*. Fig. 1. × 180.

Fig. 9.

Muscular fibres at the summit of the papilla, shewing the relation of the germinal matter to the contractile tissue, and the mode of formation of the latter by the masses of germinal matter. *a*. Germinal matter, or nucleus forming fibrillæ. *b*. Another nucleus, or mass of germinal matter, connected with muscular tissue. *c*. Germinal matter, or nucleus of fine nerve fibre distributed to the muscle near the summit of the papilla. *d*. Fine nerve fibre. × 180.

Fig. 10.

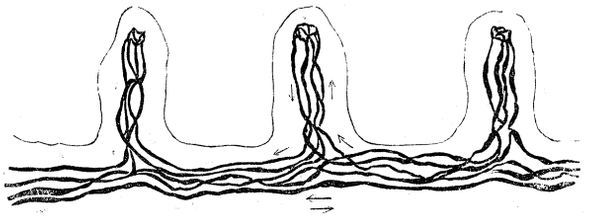
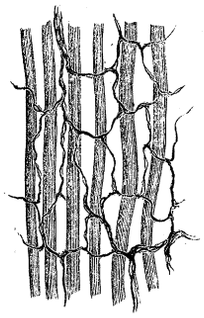


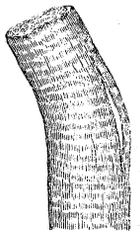
Diagram of three papillæ from the frog's tongue, to show the arrangement of the nerve fibres.

Fig. 11.



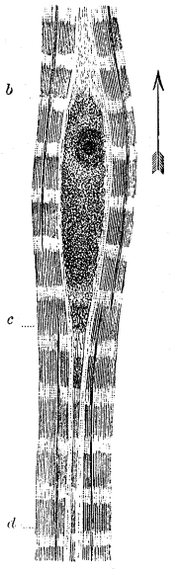
Muscular fibres from tongue, with nerve fibres ramifying amongst them.

Fig. 12.



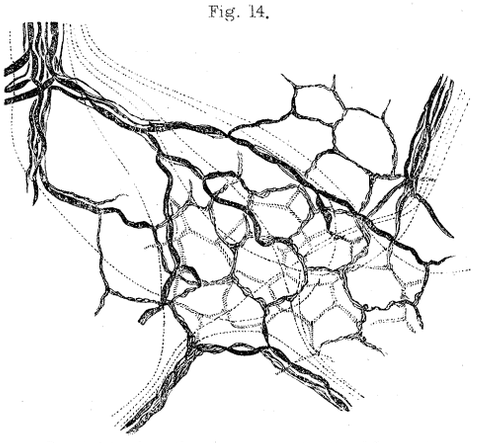
Fine muscular fibre to show a fault. × 1800.

Fig. 13.



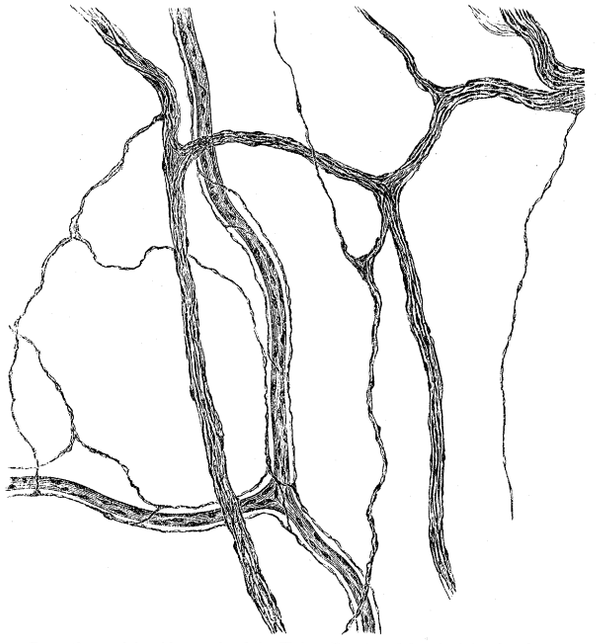
Drawing to show the mode in which the 'nucleus' takes part in the formation of the fibrillæ of muscle. The arrow shows the direction in which the nucleus moves. It once occupied the interval between *c* and *d*, but has moved to the position between *b* and *c*.

Fig. 14.



Drawing to show the plexuses or networks of fine nerve fibres. The mode of subdivision of the dark-bordered fibres, and the manner in which they enter into the formation of the plexuses, is also well seen. The course of the numerous nerve currents is indicated by the dotted lines.

Fig. 15.

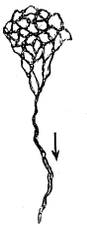


From the mylohyoid muscle of the Hyla. Trunks of fine dark-bordered nerve fibres, with fine fibres coming from them, some of which may be traced to the vessels, while others are distributed to the muscular fibres, which are not represented in the drawing. The arrangement of the nerves supplying the capillary vessel are well seen. × 110.

Fig. 16.

Mode of formation of network or plexus of finest nerve fibres.

Fig. 17.



Mode in which a single nerve fibre is supposed to terminate, according to most authors.

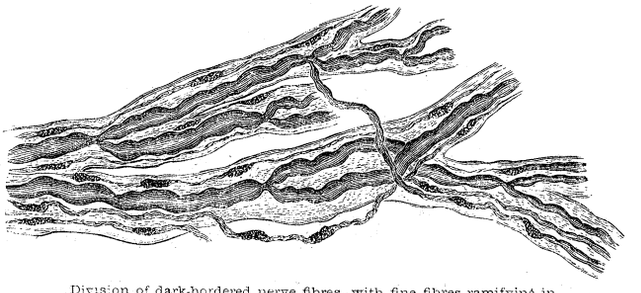
Fig. 18.

The author's view of the arrangement of the nerve fibres and formation of the terminal plexus or network of fine nerve fibres.

Fig. 19.

Arrangement of terminal pale nucleated nerve fibres in papillæ.

Fig. 20.



Division of dark-bordered nerve fibres, with fine fibres ramifying in the sheath. Breast muscle, Frog. × 300

Fig. 21.

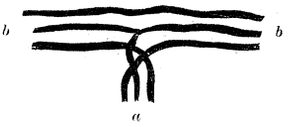
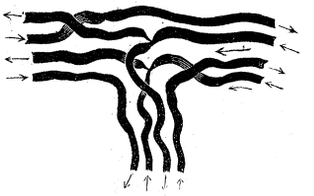
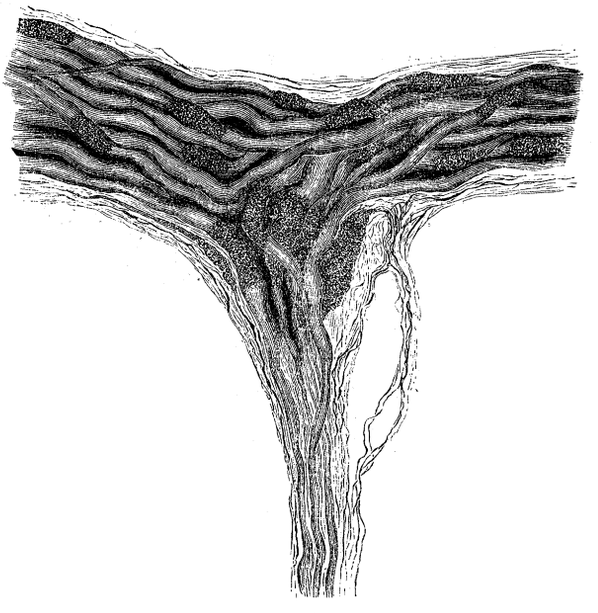


Fig. 22.



Diagrams to illustrate the course of the nerve fibres in a branch, *a*, coming off from a larger trunk *b b*.

Fig. 23.



Fine compound nerve trunk, with a branch coming off at right angles, composed of fibres which pursue opposite courses in the trunk. From the submucous tissue of the palate. Frog. × 700. 1862.